A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 100: 345–369 (2025)
DOI: 10.3897/neobiota.100.152750

Research Article

Acacia invasion triggers cascading effects above- and belowground in fragmented forests

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Abstract

Invasive alien plants like *Acacia* species are key drivers of ecosystem change, with considerable effects on forest structure, nutrient cycling, and biodiversity. In the Mediterranean region, which is already vulnerable to challenges such as anthropogenic forest fragmentation, *Acacia* species have become dominant invasive plants at the landscape scale. In this study, we explored the effects of *Acacia dealbata* Link, and *Acacia melanoxylon* R. Br. to a lower extent, in a fragmented forest landscape in Central Portugal. We hypothesised that *Acacia* invasion would alter vegetation structure, litter, soil, and springtail communities, with cascading effects on ecosystem dynamics. We established 25 sampling points within a 25 km^2 grid to collect data on *Acacia* invasion status, vegetation structure (cover of different plant layers and species richness), litter and soil quality (litter C/N ratio and soil organic carbon), and springtail communities (abundances of epigeic, hemiedaphic, and euedaphic springtails). We considered an *Acacia* invasion gradient as a continuous variable calculated with the sum of the covers of *A. dealbata* and *A. melanoxylon* divided by the total tree cover to study the combined effect of the two species. High levels of *Acacia* invasion were associated with reduced herb cover and plant species richness. Moreover, as *Acacia* invasion intensified, there was a significant decrease in the litter C/N ratio, and an increase in soil organic carbon. Subsequently, these *Acacia*-induced impacts triggered cascading effects on the relationships between shrub cover, litter and soil quality, and springtail functional structure. These findings showed that even low levels of *Acacia* invasion altered above- and belowground dynamics, thereby highlighting the cascading impacts of these invasive alien plant species on ecosystem functioning. Prioritizing early intervention in areas with smaller infestations (i.e., especially in fragmented landscapes like those in Central Portugal) can help prevent further spread and impacts of both *A. dealbata* and *A. melanoxylon*.

Key words: *Acacia dealbata*, *Acacia melanoxylon*, litter C/N ratio, soil organic carbon, springtail communities, understory

OPEN ACCESS

Academic editor: Elizabeth Wandrag
Received: 12 March 2025
Accepted: 16 July 2025
Published: 29 August 2025

Citation: Juan-Ovejero R, Reis F, Martins da Silva P, Marchante E, Garcia F, Dias MC, Covelo F, Alves da Silva A, Freitas H, Sousa JP, Alves J (2025) *Acacia* invasion triggers cascading effects above- and belowground in fragmented forests. NeoBiota 100: 345–369. https://doi.org/10.3897/neobiota.100.152750

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Introduction

Biological invasions are a significant component of global environmental change and are among the leading drivers of biodiversity loss worldwide (Bellard et al. 2016; Roy et al. 2024). Invasive alien species negatively affect ecosystems across all biogeographic regions, disrupting natural processes such as trophic interactions

and habitat structure (Pyšek and Richardson 2010; Pyšek et al. 2020). Many well-established invaders are now expanding their ranges, driven by multiple factors, including climatic and land use changes, spreading into new areas, and causing severe ecological and socio-economic impacts (Robinson et al. 2020). This problem is especially critical in forest ecosystems, as they provide essential services like carbon sequestration, water regulation, and habitat provision, all of which are crucial for sustaining human well-being (IPBES 2024).

Among the diverse array of invasive alien species, invasive plants promote significant negative impacts on forest ecosystems due to their ability to establish rapidly and dominate over the existing vegetation (Richardson and Rejmánek 2011; Vilà et al. 2011). Some invasive alien plant species are particularly troublesome because they are equipped with functional traits that were previously absent in the ecosystem, further enhancing their competitive advantage (Dyderski and Jagodziński 2019; Mathakutha et al. 2019). Consequently, when invasive alien plants dominate over native species, they can transform the structure and function of forests, resulting in the long-term degradation of these ecosystems (Liebhold et al. 2017; Wardle and Peltzer 2017). In the field of invasion ecology, these impactful species are referred to as *transformers* (*sensu* Richardson et al. 2000) and are particularly concerning because they can modify processes like nutrient, carbon, and water cycling, and reshape the composition and structure of biological communities (e.g., Rossiter-Rachor et al. 2009; Foxcroft et al. 2019; Gentili et al. 2022).

A prominent example of *transformer* species are *Acacia* trees, whose capacity to fix atmospheric nitrogen drastically alters nutrient dynamics in forest ecosystems (Richardson et al. 2023). This trait, combined with their ability to form dense stands, allows *Acacia* species to transform landscapes, altering vegetation structure and creating serious problems for large-scale forest management (Richardson et al. 2023). Previous studies have shown that *Acacia* species can outcompete native vegetation and suppress the regeneration and persistence of native herbaceous and shrub layers, often leading to a substantial loss of understory cover across invaded areas (e.g., Rascher et al. 2011; Lorenzo et al. 2012). Beyond altering vegetation and higher trophic levels (Ferreira et al. 2021), *Acacia* species also affect litter and soil characteristics, which can cascade through the ecosystem (Marchante et al. 2009; López-Núñez et al. 2017; Souza-Alonso et al. 2017). Interestingly, while *Acacia* litter may temporarily increase soil organic carbon (SOC) after invasion, its resistance to decomposition can slow organic matter turnover, potentially reducing SOC over time (Marchante et al. 2009, 2019). Such modifications may reverberate through belowground communities, disrupting the activity of decomposers that play essential roles in nutrient cycling and organic matter decomposition (Berg and Bengtsson 2007; García-Palacios et al. 2013; Bardgett and Van Der Putten 2014; Ferreira et al. 2021).

Springtails (Hexapoda, Collembola) are a highly abundant group of belowground decomposers, playing an essential role in nutrient cycling and maintaining soil-litter dynamics in forest ecosystems, which makes them excellent indicators of environmental change (Fujii and Takeda 2012). They are functionally grouped based on vertical stratification and resource-acquisition strategies used to access organic matter, nutrients, and moisture in the soil: *epigeic* springtails move across the soil surface and exploit litter; *hemiedaphic* springtails reside in litter but are able to migrate to upper soil layers; and *euedaphic* springtails inhabit deep soil layers with fewer fluctuations in temperature and moisture than those closer to the sur-

face (Gisin 1960; Rusek 1998; Petersen 2002). Springtail communities are highly sensitive to changes in resource availability and substrate quality, and can act as a small yet powerful biological lens for understanding forest ecosystem dynamics (Auclerc et al. 2009; Pollierer and Scheu 2017; Gruss et al. 2023). For example, genus-specific leaf litter traits have a greater impact on their assembly than tree species origin in young plantations (Raymond-Léonard et al. 2018), and bamboo invasions alter their composition and functional structure through changes in litter quality (Long et al. 2023). The use of these soil animals as functional indicators to study the belowground effects of *Acacia* invasion is particularly novel in this context. This approach is useful because springtail functional groups respond rapidly to changes in litter and soil quality (Potapov et al. 2016), which are factors that can be directly influenced by invasive litter and soil inputs. *Acacia* litter may limit the palatability of surface resources, likely disadvantaging epigeic and hemiedaphic springtails. In contrast, euedaphic species may be better adapted to the recalcitrant carbon characteristic of deep layers in *Acacia*-invaded soils.

Many *Acacia* species thrive in nutrient-poor soils and grow rapidly in favourable climates like that of the Mediterranean Basin, where their rapid proliferation presents considerable management challenges (Souza-Alonso et al. 2017; Vieites-Blanco and González-Prieto 2020; Marchante et al. 2023). Although the negative effects of *Acacia* invasion are well-documented at the habitat scale in this region, including impacts on communities of plants (Lorenzo et al. 2011; Marchante et al. 2015; da Silva et al. 2019), birds (Nereu et al. 2024), invertebrates (López-Núñez et al. 2017; da Silva et al. 2019; Nereu et al. 2024), and microbial functioning (Marchante et al. 2009; Lorenzo et al. 2010a; Lazzaro et al. 2014; Souza-Alonso 2014; 2015), broader studies that assess their effects across multiple vegetation types in fragmented Mediterranean landscapes remain scarce. This knowledge gap is especially pressing in countries like Portugal, where *Acacia* invasion is particularly severe, with the highest number of invasive *Acacia* species in the Mediterranean (i.e., ten recorded to date; Marchante et al. 2023). The characteristics of *Acacia* species, combined with forest fragmentation due to rural land abandonment, increasing fire risk, and the expansion of large-scale monoculture plantations, have heightened the vulnerability of Portuguese forest ecosystems to invasion by these species (Marchante et al. 2023). This emphasizes the need to study invasion gradients across landscapes to gain a clearer understanding of how *Acacia* invasions may transform ecosystem dynamics.

In this study, we aimed to assess the impacts of *Acacia dealbata* Link., and *Acacia melanoxylon* R. Br. to a lower extent, in a fragmented forest landscape with varying invasion levels in Central Portugal. We seek to address key knowledge gaps by highlighting belowground impacts of *Acacia* invasion, an area still less explored compared to aboveground effects. In addition, the integrative focus on cascading effects across ecosystem compartments, together with the landscape-scale approach, allows for a more comprehensive understanding of the spatial dynamics of biological invasions in fragmented forest ecosystems. Our hypotheses reflect potential pathways through which *Acacia* invasion may transform ecosystem dynamics. We expect that *Acacia* invasion would change vegetation structure by reducing herb and shrub cover (i.e., understory) and plant species richness (H_1). Moreover, as a consequence of H_1, we hypothesise that invasion of *Acacia* trees would alter litter and soil characteristics by decreasing the litter C/N ratio and increasing soil organic carbon (SOC) (H_2). Also, we expect that

Acacia invasion would lead to shifts in springtail functional structure, resulting in changes in the abundances of epigeic, hemiedaphic, and euedaphic springtails (H_3). Finally, as a combined consequence of the three previous hypotheses, we expect that *Acacia*-invaded areas within the fragmented forest landscape would experience cascading effects: plant communities become more homogeneous and dominated by nitrogen-fixing *Acacia* trees, thus altering litter and soil quality, which, in turn, would affect the functional structure of springtail communities by changing their resource-acquisition strategies (H_4).

Material and methods

Study site

The study area was located in the Lousã mountains (40°3'N, -8°15'W, central Portugal; Fig. 1a), covering a surface of 170 km^2 with an elevation ranging between 100 and 1,205 m a.s.l. The climate in the area is classified as Mediterranean. However, the geographic location (i.e., close to the Atlantic Ocean) and topography (i.e., steep hills and valleys) in the Lousã mountains lead to higher precipitation levels than those that are typical for classic Mediterranean regions (Mora and Vieira 2020). The annual mean temperature is 16 °C, the annual mean minimum and maximum temperatures are 10 °C and 23 °C, respectively, and the annual precipitation varies between 650 and 1000 mm (climatic data from 2000 to 2022, from the nearest meteorological station (IPMA 2025). In recent decades, this area has undergone remarkable changes due to the natural regrowth of forests on abandoned agricultural lands, the establishment of monoculture plantations, forest fires, and the spread of non-native *Acacia* species, including *A. dealbata* and *A. melanoxylon*. *A. dealbata* has bipinnate compound leaves, and contrasts morphologically with *A. melanoxylon*, which possesses thick phyllodes (i.e., widened and flattened petiole with the appearance of a leaf blade) (Bentham 1875; Murphy and Maslin 2023). These *Acacia* species were originally planted along roadsides for ornamental reasons and erosion prevention but have expanded beyond their original locations. In most of the Lousã mountains area, *A. dealbata* is the dominant species, but *A. melanoxylon* is also common. Importantly, *A. dealbata* is much more widespread, possibly due to its invasion history and higher propagule pressure, as it was more widely used (Montesinos et al. 2016; da Silva et al. 2019; Garcia et al. 2023).

In spring 2023, a 25 km^2 grid was overlaid on the study area and further divided into 25 individual square segments, each measuring 1 km^2 (Fig. 1b, c). The grid covered an invasion gradient of *A. dealbata*, and *A. melanoxylon* to a lower extent, across a diverse range of vegetation types that included: conifer stands with monoculture plantations of maritime pine (*Pinus pinaster* Aiton; native), European black pine (*Pinus nigra* J.F.Arnold; alien, non-invasive), Scots pine (*Pinus sylvestris* L.; alien, non-invasive), Lawson cypress (*Chamaecyparis lawsoniana* (A.Murray bis) Parl.; alien, non-invasive) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco; alien, non-invasive); planted birch stands (*Betula pubescens* Ehrh.; alien, non-invasive), broadleaf natural forests of Orocantabrian oak (*Quercus orocantabrica* Rivas Mart., Penas, T.E.Díaz & Llamas; native), chestnut (*Castanea sativa* Mill.; alien, non-invasive) and strawberry tree (*Arbutus unedo* L.; native); and Mediterranean shrublands with evergreen shrubs such as bramble broom (*Genista tridentata* L.;

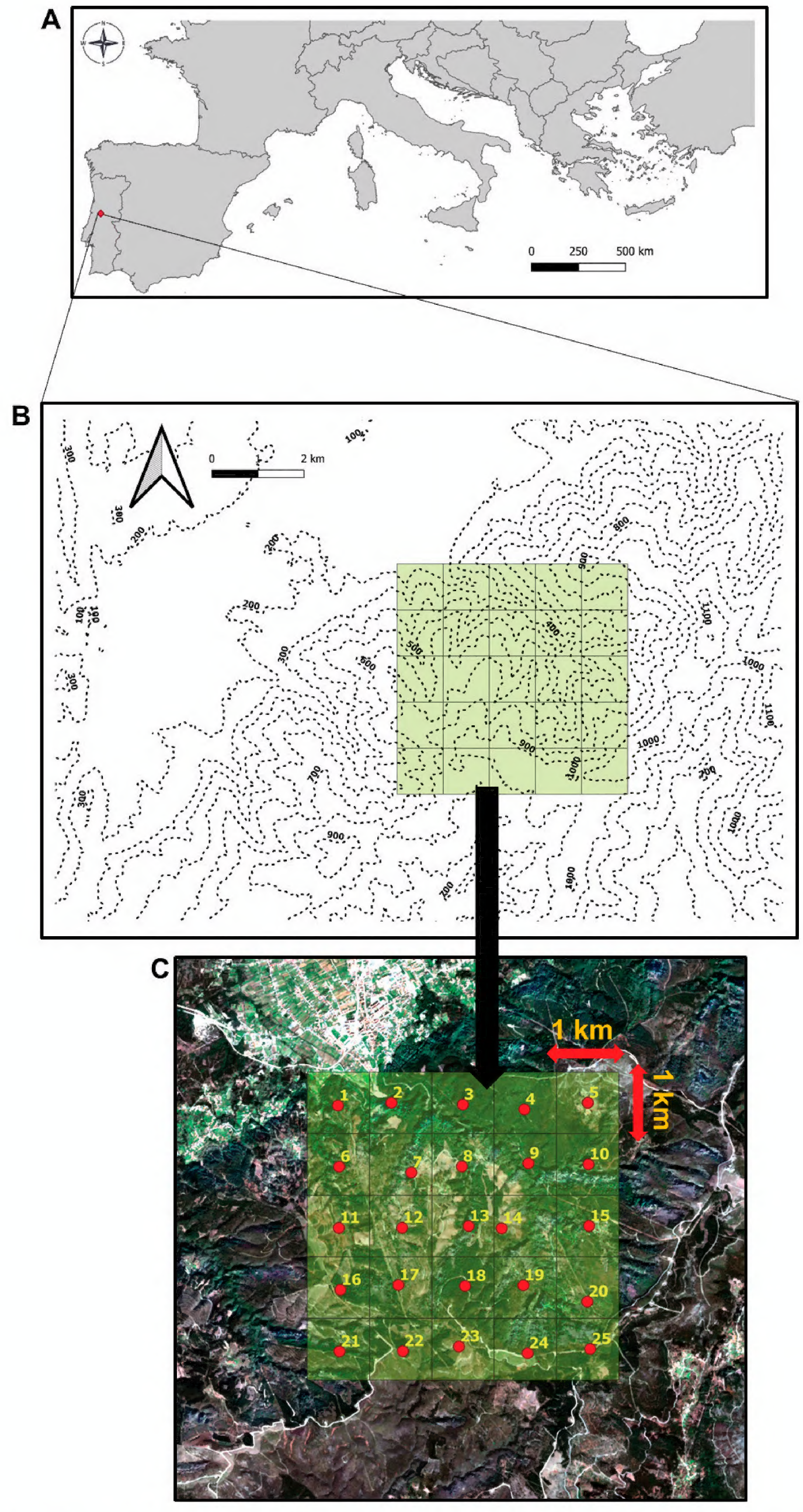

Figure 1. A. Location of the study area within the Mediterranean Basin and Portugal; **B.** Sample area, showing the grid with 25 regular square segments and dashed lines showing the contour lines (i.e., connecting points of equal elevation) in 100 m intervals, and **C.** Exact location of the 25 sampling points (red dots) within the 25 km^2 grid.

native), bristle-leaved heath (*Erica umbellata* L.; native) and gorse (*Ulex minor* Roth; native).

A total of 25 sampling points were established within the grid, with one point allocated to each 1 km^2 square; in each of these, data on vegetation structure, litter and soil quality, and springtail functional structure were gathered. Sampling points were selected as near as possible to the center of each sampling square, with small adjustments due to accessibility (Fig. 1c).

The coordinates, information on topographic variables (elevation, slope, and aspect; LNEG 2025) and *Acacia* invasion status (invaded or non-invaded) of each sampling point were recorded (Table 1). Of the 25 sampling points, nine were invaded (with a cover of *Acacia*, including *A. dealbata* and/or *A. melanoxylon*, of at least 5%; Table 1) and the remaining 16 showed no signs of invasion.

Table 1. Coordinates, elevation, slope, aspect, dominant vegetation type, *Acacia* invasion status, *Acacia* cover (considering *A. dealbata* and *A. melanoxylon*), and proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance at each sampling point. *Acacia* cover (%) may exceed 100% due to overlapping canopies of *A. dealbata* and *A. melanoxylon*.

Sampling point	Coordinates	Elevation (m a.s.l.)	Slope (%)	Aspect (°C)	Dominant vegetation type	*Acacia* invasion status	*Acacia* cover (%)	Proportion of *Acacia* cover (%)
1	40.099459°N, -8.252573°W	150	15	13	*Pinus pinaster* plantation	Invaded	30% *A. dealbata* + 15% *A. melanoxylon*	38
2	40.099788°N, -8.242508°W	152	41	12	*Arbutus unedo* natural stand	Non-invaded	0	0
3	40.099436°N, -8.229062°W	155	13	202	*Acacia* stands	Invaded	100% *A. dealbata*	100
4	40.098660°N, -8.217495°W	157	23	248	*Acacia* stands	Invaded	95% *A. dealbata* + 40% *A. melanoxylon*	100
5	40.099548°N, -8.205552°W	160	17	199	*Quercus orocantabrica* natural stand	Non-invaded	0	0
6	40.090503°N, -8.252446°W	517	30	294	*Pinus pinaster* plantation	Invaded	10% *A. melanoxylon*	43
7	40.089575°N, -8.238877°W	573	21	279	*Quercus orocantabrica* natural stand	Non-invaded	0	0
8	40.090394°N, -8.22936°W	526	23	56	*Pinus pinaster* plantation	Invaded	15% *A. dealbata*	18
9	40.090768°N, -8.216838°W	408	16	284	*Acacia* stands	Invaded	95% *A. dealbata*	100
10	40.090542°N, -8.205543°W	540	24	10	Shrubland	Invaded	20% *A. dealbata*	57
11	40.081559°N, -8.252607°W	605	19	32	*Pinus pinaster* plantation	Non-invaded	0	0
12	40.081508°N, -8.240706°W	691	15	274	Shrubland	Non-invaded	0	0
13	40.081659°N, -8.228194°W	669	30	317	*Pinus pinaster* plantation	Non-invaded	0	0
14	40.081293°N, -8.22198°W	654	26	151	*Pinus pinaster* plantation	Invaded	20% *A. dealbata*	57
15	40.081536°N, -8.205533°W	595	16	7	*Quercus orocantabrica* natural stand	Non-invaded	0	0
16	40.072491°N, -8.252415°W	774	13	234	*Chamaecyparis lawsoniana* + *Pinus nigra* plantation	Non-invaded	0	0
17	40.073124°N, -8.241503°W	862	23	289	*Castanea sativa* natural stand	Non-invaded	0	0
18	40.072903°N, -8.22895°W	855	17	59	*Pinus pinaster* plantation	Non-invaded	0	0
19	40.072924°N, -8.217977°W	676	22	43	*Pinus pinaster* plantation	Non-invaded	0	0
20	40.070458°N, -8.205991°W	890	25	348	Shrubland	Invaded	5% *A. dealbata*	20
21	40.063488°N, -8.252684°W	740	23	233	*Pseudotsuga menziesii* plantation	Non-invaded	0	0
22	40.063447°N, -8.24077°W	871	9	124	*Pinus nigra* plantation	Non-invaded	0	0
23	40.064056°N, -8.230222°W	924	12	270	*Betula pubescens* plantation	Non-invaded	0	0
24	40.062979°N, -8.217285°W	970	10	339	Shrubland	Non-invaded	0	0
25	40.063524°N, -8.205514°W	988	8	174	*Pinus nigra* plantation	Non-invaded	0	0

Plant surveys

At each sampling point, three quadrats of varying dimensions were used to sample vascular plants, arranged in a nested structure from smallest to largest. Specifically, a 2 × 2 m quadrat was used for herbs, a 3 × 3 m quadrat for shrubs, and a 10 × 10 m quadrat for trees (also used to assess *Acacia* invasion status). The total number of quadrats of each size was 25, with the smaller quadrats nested within the larger ones. The cover of each species was visually estimated in 5% intervals, and when lower than that it was assessed in shorter intervals. We followed the plant nomenclature established by POWO (2025). The cover of each vegetation layer (trees, shrubs and herbs) was measured at each sampling point as the sum of the cover of all plant species within each growth form. These covers can exceed 100% due to overlapping species within the same growth form. Furthermore, we calculated the overall plant species richness at each sampling point by adding up all plant species observed. To quantify the extent of *Acacia* invasion, we calculated a continuous *Acacia* invasion gradient as the proportion of *Acacia* relative to total tree abundance by dividing the combined cover of *Acacia* species (*A. dealbata* + *A. melanoxylon*) by the total tree cover at each sampling point. Due to the remarkably lower proportion of *A. melanoxylon* compared to *A. dealbata*, and its limited distribution to specific sampling points (n = 3, Table 1), we combined the two *Acacia* species for our analyses, thereby ensuring sufficient statistical robustness. This calculated proportion provided insight into *Acacia*'s dominance relative to other tree species, helping to assess its invasion status within the fragmented forest landscape. Furthermore, by examining this proportion, we gained a better understanding of how varying levels of *Acacia* invasion might influence the understory (i.e., herb and shrub cover).

Litter and soil quality

Since the litter C/N ratio is a reliable predictor of litter turnover (Delgado-Baquerizo et al. 2015) and soil organic carbon (SOC) gives information about the ability of soils to store carbon (Lal 2004), they were used as litter and soil quality indicators, respectively. Two quadrats of 25 × 25 cm were used at each sampling point to collect litter down to the mineral soil (i.e., the entire decomposing forest floor, excluding the underlying mineral soil; Gillespie et al. 2021), totaling 50 samples. This collection method focused on the litter layer specifically, which is composed of decomposing plant material, rather than the soil organic matter that is integrated with the mineral soil. The two 25 × 25 cm quadrats per sampling plot were established at the exact coordinates (latitude and longitude) listed in Table 1. Litter samples were oven-dried at 65 °C and ground to powder (~1 mm) for homogenization. Total carbon and nitrogen contents (%) were determined using a CN 802 Carbon Nitrogen Elemental Analyzer (VELP Scientifica, Usmate Velate, Italy) at the Centre for Functional Ecology, University of Coimbra (Portugal).

After removing the litter from each 25 × 25 cm quadrat, one soil sample was collected with a PVC core (Ø 5 cm x 5 cm depth), totaling again 50 samples. Soil was oven-dried at 105 °C and subsequently sieved through a 2 mm mesh. Soil organic carbon content (%) was measured following digestion with HCl using the same analyzer as above.

Springtail extraction and classification into functional groups

At each of the same sampling points, two samples were collected using PVC cores (Ø 5 cm x 5 cm depth), including both soil and litter, to sample springtail communities, totaling 50 samples. Samples were placed in plastic bags and kept cool (~4 °C) until extraction (i.e., within 24 hours). Springtails were extracted in a Macfadyen high-gradient extractor during 4 days (Sousa et al. 2004). Afterwards, specimens were preserved in 96% ethanol in plastic vials and counted with a binocular stereo microscope. Each springtail specimen was classified into one of the following functional types: *epigeic*, *hemiedaphic*, or *euedaphic*. For this classification, a range of eco-morphological traits reflecting springtail adaptations to the soil profile was used: i) the presence or absence of ocelli, ii) antennae length, iii) furca characteristics (presence/absence and length), iv) the presence of scales or thick hairs along the body, and v) body pigmentation (Parisi et al. 2005; Vandewalle et al. 2010; Martins da Silva et al. 2016, 2023; Reis et al. 2016). To specifically classify each specimen into a functional type, each morphological trait was assigned a score from 0 to 4 (see Suppl. material 1: table S2 for detailed information). After assigning scores to each trait, a composite life-form trait was calculated by summing the partial scores of each functional type, and then this was divided by the maximum possible score of 20 so that each life-form trait has a continuous value varying between 0 and 1. This normalization allowed each individual to have a single life-form trait score ranging from 0 to 1 (Martins da Silva et al. 2016, 2023), with higher scores indicating a greater adaptation of springtails to the soil profile (i.e., from 0 to 0.3 for epigeic springtails; from 0.4 to 0.6 for hemiedaphic springtails; and from 0.7 to 1 for euedaphic springtails; Suppl. material 1: table S2). The number of specimens of each functional type found in each sample was divided by the surface of the core (19.625 cm^2), and the abundances of epigeic, hemiedaphic, and euedaphic springtails were then expressed as individuals per square meter of soil.

Statistical analyses

We conducted two preliminary analyses to assess any possible impact of spatial patterns and the physical environment on *Acacia* invasion within the fragmented forest landscape. First, we applied a Moran's I test using the "ape" package (Paradis and Schliep 2019) to evaluate spatial autocorrelation in the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance across sampling points. Second, we used Spearman correlation tests to examine the specific relationships between the proportion of *Acacia* relative to total tree abundance with latitude, longitude, elevation, slope, and aspect. After detecting significant spatial autocorrelation in the proportion of *Acacia* cover (observed Moran's I statistic: 0.064; expected Moran's statistic: -0.042; p-value < 0.001), and significant correlations of latitude and elevation with the proportion of *Acacia* cover (Suppl. material 1: table S3), we tested our four hypotheses (Fig. 2) as detailed below. H_1, H_2, and H_3 considered the entire landscape, which included both invaded and non-invaded areas, while H_4 focused specifically on the sampling points invaded by *Acacia*.

To test H_1, we ran independent generalized linear models (GLMs) with a negative binomial family, using herb cover, shrub cover, and plant species richness as response variables. The proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover

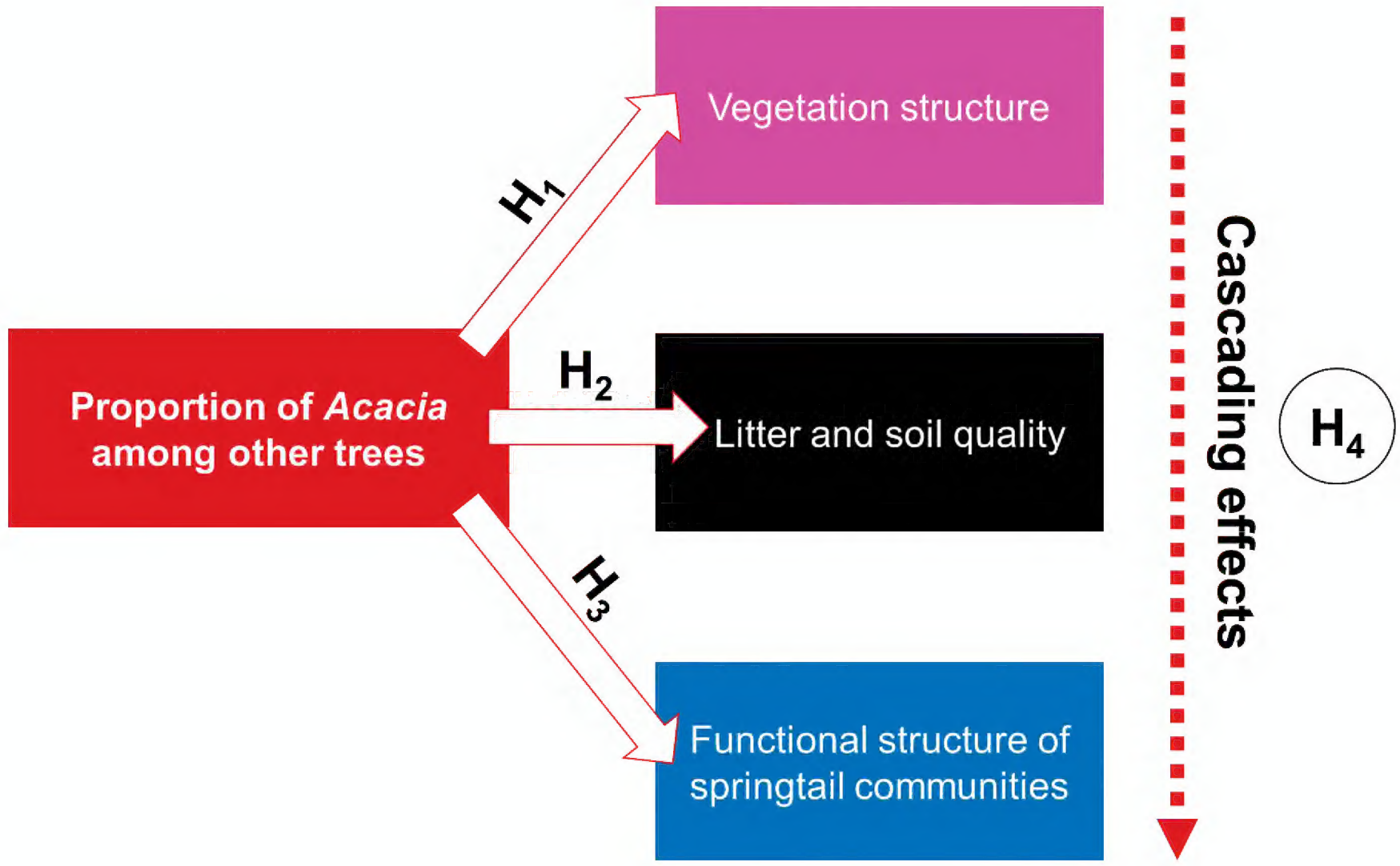

Figure 2. Conceptual flow chart showing the hypotheses of the study. Expected effects of *Acacia* invasion: (H_1) reduce understory cover (herb and shrub layers) and plant species richness; (H_2) alter litter and soil characteristics, with a lower litter C/N ratio and increased soil organic carbon (SOC); (H_3) shift in springtail functional structure, affecting the abundances of epigeic, hemiedaphic, and euedaphic groups; and (H_4) cascading effects, where *Acacia*-invaded areas become more homogeneous and dominated by nitrogen-fixing trees, leading to changes in litter and soil quality that influence springtail resource-acquisition strategies.

was the predictor variable, and latitude and elevation were included as covariates. Additionally, using the covers of each plant species, we compared plant community assemblages between *Acacia*-invaded and non-invaded sampling points by conducting non-metric multidimensional scaling (NMDS) based on the Bray-Curtis similarity index, and we subsequently evaluated the dissimilarities observed with a similarity percentage analysis (SIMPER).

To test H_2, we conducted independent GLMs with a negative binomial family for the litter C/N ratio and SOC as response variables, and the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover was the predictor variable, with latitude and elevation included as covariates.

To test H_3, we fitted a single GLM with a Gaussian family to evaluate how springtail abundances responded to changes in the proportion of *Acacia* cover (*A. dealbata* + *A. melanoxylon*) across functional groups (epigeic, hemiedaphic and euedaphic). Springtail abundances were transformed to log(x+1) to meet normality criteria, and we used a zero-inflated model to account for the high number of zero values in the abundance data. Functional group was included as a categorical grouping factor, and the interacton term between functional group and the proportion of *Acacia* cover was used to test whether the effect of *Acacia* varied among groups. Latitude and elevation were also included as covariates.

To test H_4, we performed two analyses. To evaluate how changes in vegetation structure affect litter and soil characteristics, we used independent GLMs with a negative binomial family, with litter C/N ratio and SOC as response variables. Each predictor variable (i.e., herb cover, shrub cover and plant species richness) was

used independently in separate models. Moreover, to evaluate how changes in litter and soil characteristics affect the functional structure of springtail communities, we performed independent GLMs with a Gaussian family. In these models, the abundances of epigeic, hemiedaphic, and euedaphic springtails were the response variables, while the litter C/N ratio and SOC were used as independent predictor variables in separate models. As in H_3, we log-transformed springtail abundances.

All generalized linear models (GLMs) were conducted using the "glmmTMB" package (Brooks et al. 2017). We assessed the significance of latitude and elevation as covariates across all models for H_1, H_2, and H_3 by performing step-by-step model selections (Crawley 2012). Specifically, we started with a full model that included the proportion of *Acacia* cover, latitude, and elevation as predictor variables, and we then progressively simplified the model by removing non-significant variables (reduced model). Model comparisons were based on Akaike Information Criterion (AIC), selecting the model with the lowest AIC, and using ANOVA likelihood-ratio tests to ensure that the selected models significantly improved the fit (p-value < 0.05). Graphical assessments were then performed to confirm the normality and homogeneity of the residuals for each final model. All analyses were conducted using R (R 3.6.2, R Core Team 2024) except NMDS and SIMPER, which were run with Primer v6 (Clarke and Warwick 2001).

Results

Effects of *Acacia* invasion on vegetation structure (H_1)

As the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover increased, herb cover decreased significantly (Estimate = -0.037, z = -3.837, p-value < 0.001; Fig. 3a). Additionally, latitude (Estimate = 124.760, z = 2.450, p-value = 0.014; Suppl. material 1: fig. S2a) and elevation (Estimate = 0.006, z = 2.337, p-value = 0.019; Suppl. material 1: fig. S2b) were found to positively affect herb cover. While the full model showed marginally more significance than the model with only the proportion of *Acacia* cover, it also had the lowest AIC among all models tested (Suppl. material 1: table S4). In contrast, the proportion of *Acacia* cover did not significantly affect shrub cover (Estimate = -0.016, z = -1.033; p-value = 0.301) in either the full model or the reduced models (Fig. 3b; Suppl. material 1: table S4).

When assessing plant species richness, we found that the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover had a significant negative effect, with higher proportion of *Acacia* associated with lower plant richness (Estimate = -0.007, z = -2.012, p-value = 0.044; Fig. 3c). The model using only the proportion of *Acacia* cover as a predictor variable was identified as the best fit, showing the lowest AIC (129.7) among all models tested (Suppl. material: table S4).

A. dealbata and *A. melanoxylon* were found growing together at two sampling points, while *A. dealbata* was recorded alone at six points and *A. melanoxylon* at only one (Table 1). The lowest proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover was 18%, and *A. melanoxylon* was found in lower proportions than *A. dealbata* across the whole fragmented forest landscape (Table 1). Moreover, we found considerable differences in plant species assemblages between invaded and non-invaded sampling points (Suppl. material 1: fig. S1). The SIMPER analysis (Suppl. material 1: table S5) showed an average dissimilarity of 90.41% between these two groups. The species contributing most to this dissimilarity was

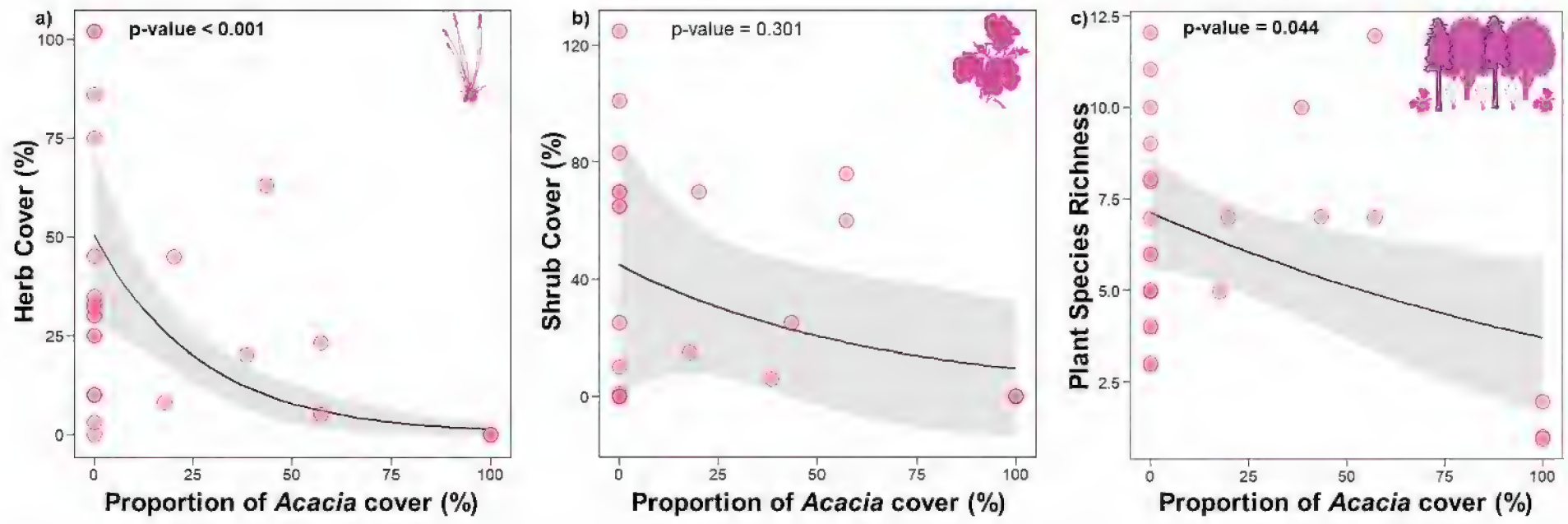

Figure 3. Scatterplots showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance with vegetation structure (H_1): **A.** Herb cover; **B.** Shrub cover, and **C.** Plant species richness. The regression lines of best fit are derived from each GLM analysis. The solid line shows the model prediction, and the grey shaded region represents the 95% confidence interval for those predictions. P-values highlighted in bold show a significant effect of proportion of *Acacia* cover (p-value < 0.05).

A. dealbata, accounting for 18.33%. Following this, *P. pinaster* contributed with 12.56%, and several other species contributed with more than 5%, including *P. nigra*, the fern *Pteridium aquilinum* (L.) Kuhn, and the shrubs *U. minor* and *G. tridentata*. Detailed information on all surveyed vascular plants is shown in Suppl. material 1: table S1.

Effects of *Acacia* invasion on litter and soil quality (H_2)

As the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover increased, the litter C/N ratio decreased significantly (Estimate = -0.003, z = -2.214, p-value = 0.027; Fig. 4a). In contrast, latitude (Estimate = 22.941, z = 2.671, p-value = 0.008; Suppl. material 1: fig. S3a) and elevation (Estimate = 0.001, z = 3.079, p-value = 0.002; Suppl. material 1: fig. S3b) were found to positively influence the litter C/N ratio. Model comparisons showed that the full model provided a significantly better fit than the reduced models (Suppl. material 1: table S4). Contrarily, as the proportion of *Acacia* cover increased, soil organic carbon (SOC) increased significantly (Estimate = 0.003, z = 2.020, p-value = 0.043; Fig. 4b). Although the full model with latitude and elevation showed the lowest AIC, it did not improve the fit, as these two covariates were not significant (Suppl. material 1: table S4).

Effects of *Acacia* invasion on springtail functional structure (H_3)

The proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover did not significantly influence the overall springtail abundance (Estimate = 0.002, z = 0-62, p-value = 0.533; Fig. 5), and the interaction between functional group and proportion of *Acacia* cover was also non-significant, with any group showing responses to *Acacia* invasion. However, independently of *Acacia* presence, the model revealed significant differences among functional groups, with both hemiedaphic (Estimate = 0.84, z = 5.95, $p < 0.001$) and euedaphic springtails (Estimate = 0.79, z = 5.61, $p < 0.001$) exhibiting greater abundances than epigeic springtails. Model comparisons showed that the model including elevation as a covariate had the lowest AIC, but it did not significantly provide a better fit than the most reduced model (Suppl. material 1: table S4).

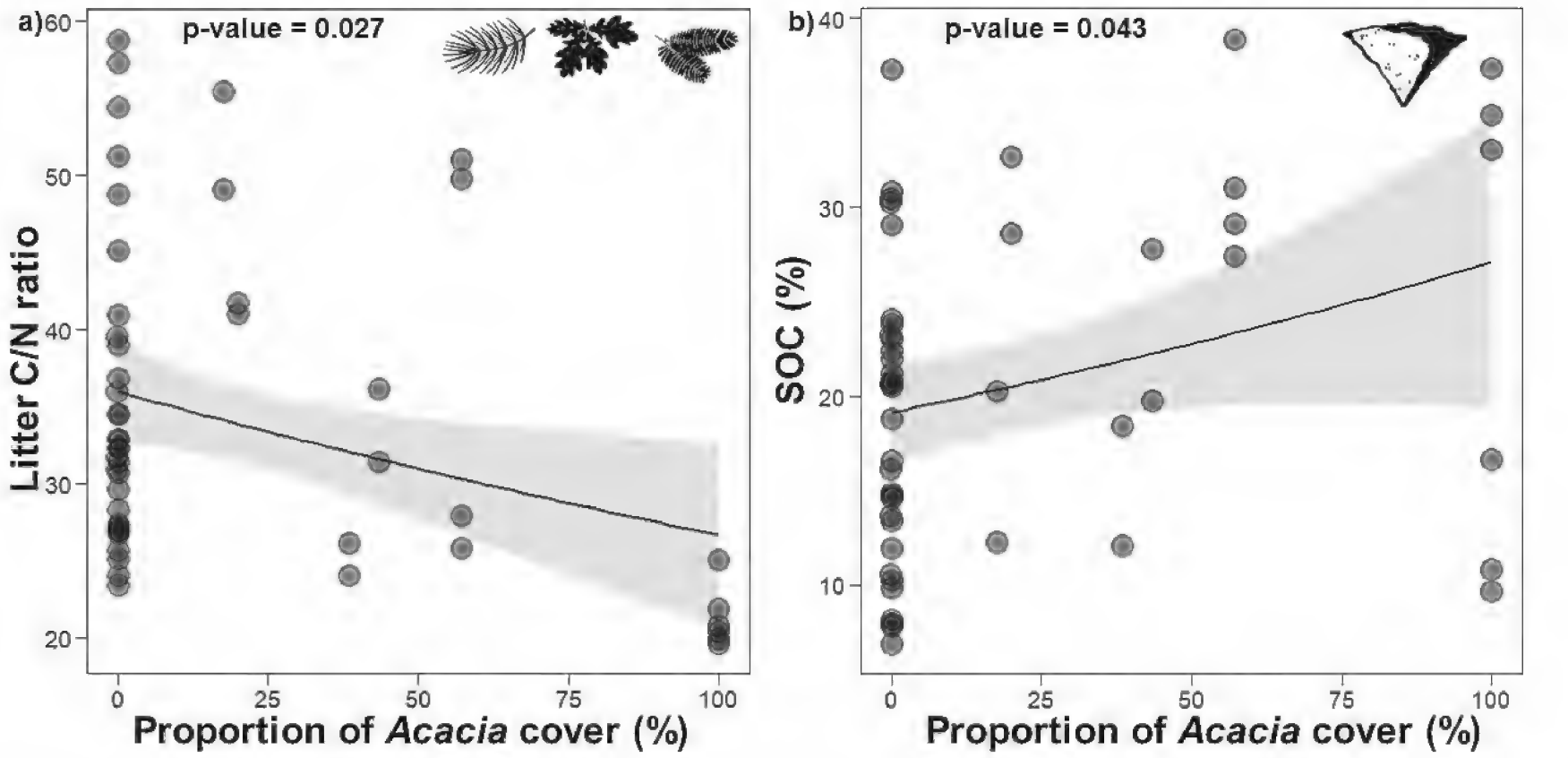

Figure 4. Scatterplots showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance with litter and soil quality (H_2): **A.** Litter C/N ratio, and **B.** SOC. The regression lines of best fit are derived from each GLM analysis. The solid line shows the model prediction, and the grey shaded region represents the 95% confidence interval for those predictions. P-values highlighted in bold show a significant effect of proportion of *Acacia* cover (p-value < 0.05).

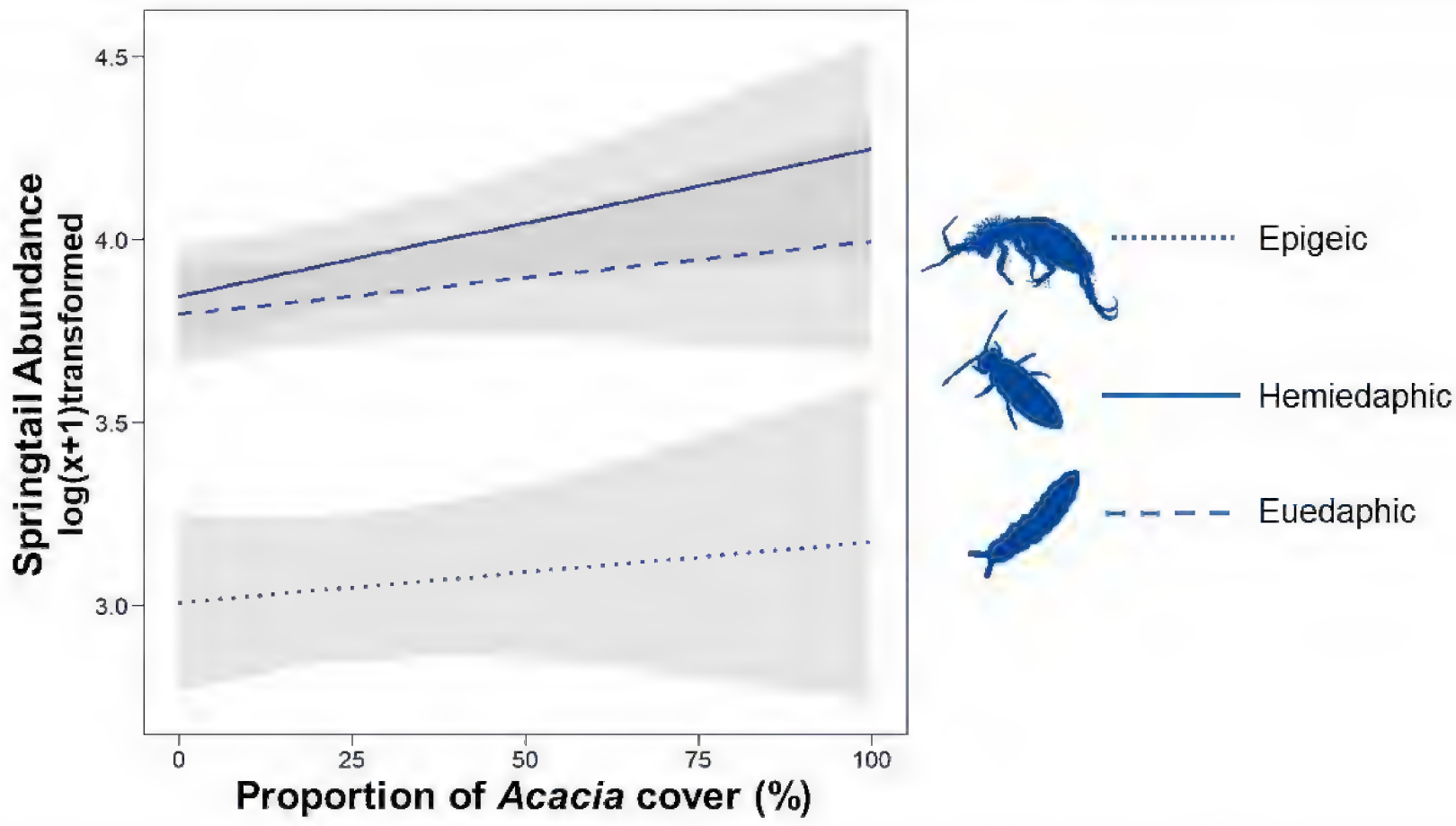

Figure 5. Scatterplot showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance across springtail functional groups (H_3): epigeic (dotted line), hemiedaphic (solid line), and euedaphic (dashed line). The regression lines of best fit are derived from the GLM analysis. The dotted, solid and dashed lines show the model predictions, and the grey shaded region represents the 95% confidence interval for those predictions. There were not any significant effects of proportion of *Acacia* cover on any springtail functional group.

Cascading effects of *Acacia* invasion (H_4)

Shrub cover significantly increased the litter C/N ratio and SOC (Table 2a), while herb cover and plant species richness had no significant effect on either litter C/N ratio or SOC (Table 2a). Moreover, when we evaluated the functional structure of springtail communities in relation to litter and soil quality in *Acacia*-invaded sampling points, we observed that for epigeic springtails, neither the litter C/N

Table 2. Summary of the GLMs assessing the the responses of i) Litter and soil quality to changes in vegetation structure and ii) Springtail functional structure to changes in litter and soil quality in *Acacia*-invaded sampling points (H_4). Signficant predictor variables for each model are highlighted in bold (p-value < 0.05).

a) Litter and soil quality responses to changes in vegetation structure				
Response variable	**Predictor variable**	**Estimate**	**z**	**p-value**
	(Intercept)	3.423	30.940	<0.001
	Herb Cover	0.003	0.830	0.407
Litter C/N ratio	**(Intercept)**	**3.301**	**31.240**	**<0.001**
	Shrub Cover	**0.006**	**2.366**	**0.018**
	(Intercept)	3.343	24.534	<0.001
	Plant Species Richness	0.032	1.297	0.195
	(Intercept)	3.170	25.248	<0.001
	Herb Cover	0.002	0.335	0.737
SOC	**(Intercept)**	**3.026**	**25.409**	**<0.001**
	Shrub Cover	**0.006**	**2.005**	**0.045**
	(Intercept)	3.139	20.893	<0.001
	Plant Species Richness	0.010	0.394	0.694
b) Springtail functional structure responses to changes in litter and soil quality				
Response variable	**Predictor variable**	**Estimate**	**z**	**p-value**
	(Intercept)	1.664	1.554	0.140
	Litter C/N ratio	-0.015	-0.486	0.634
Epigeic Springtails Abundance	(Intercept)	1.349	1.298	0.213
	SOC	-0.007	-0.179	0.860
	(Intercept)	**4.810**	**28.781**	**<0.001**
	Litter C/N ratio	**-0.025**	**-5.119**	**<0.001**
Hemiedaphic Springtails Abundance	(Intercept)	3.876	14.938	<0.001
	SOC	0.005	0.538	0.598
	(Intercept)	2.996	4.342	0.001
	Litter C/N ratio	0.021	1.047	0.311
Euedaphic Springtails Abundance	**(Intercept)**	**2.209**	**3.907**	**0.001**
	SOC	**0.060**	**2.774**	**0.014**

Degrees of freedom (d.f.) of the residuals are 15 for each model. n = 18 in all models

ratio nor SOC significantly influenced their abundance (Table 2b). However, hemiedaphic springtails showed a significant negative response to increasing litter C/N ratio, but not to SOC levels (Table 2b). Contrarily, euedaphic springtails responded positively to higher SOC levels, although the litter C/N ratio did not significantly affect their abundance (Table 2b).

Discussion

In the fragmented forest landscape, *Acacia* invasion altered vegetation structure (H_1) and litter and soil quality (H_2), thereby triggering cascading effects on the links between shrub cover, litter and soil characteristics, and springtail functional structure (H_4). Nevertheless, direct impacts of *Acacia* invasion on springtail groups were not significant (H_3). Altogether, these findings highlight that invasive alien plants influence not only plant communities but also the broader litter-soil continuum dynamics (Marchante et al. 2009, 2019; Ferreira et al. 2021).

Acacia invasion modified vegetation structure (H_1)

The occurrence of *A. dealbata* and *A. melanoxylon* at the landscape scale was associated with a significant reduction in herb cover and plant species richness. These results align with da Silva et al. (2019), who found that even moderate *Acacia* invasion can alter understory vegetation structure in the same study area. Additionally, the impact of *Acacia* presence on herb cover varied with topographic factors such as elevation and latitude, likely due to their influence on light availability for *A. dealbata* (Lorenzo et al. 2010b) and other species with phyllode-like leaves like *A. melanoxylon* (Unwin et al. 2006). These spatial patterns highlight the interaction between invasion-driven biological changes and broader physical landscape characteristics (Ohlemüller et al. 2006; Heringer et al. 2020). Nevertheless, replication within specific vegetation types was limited (Table 1), preventing us from including this category as a factor in our analyses. Therefore, future studies should ensure adequate replication across vegetation types at the landscape level to detect any specific invasion effects.

We expected a negative effect of *Acacia* proportion (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance on shrub cover in the fragmented forest landscape. Although we observed a generally negative relationship between *Acacia* invasion and shrub cover, this was not statistically significant. This may be because several sampling points lay in transitional zones where *Acacia* trees and native shrubs coexisted (Suppl. material 1: table S1). In such mixed zones, shrub cover values were more variable, which diluted the contrast with fully *Acacia*-invaded or fully shrub-dominated sampling points and reduced statistical power to detect a clear effect. Importantly, *U. minor* and *G. tridentata* were identified as key contributors to the differences between invaded and non-invaded areas. Although their contributions to overall dissimilarity were relatively low (< 7%), these species are important for understanding the observed patterns. Both are nitrogen-fixing and were less abundant in invaded areas, suggesting that they may occupy similar niches such that *Acacia* pre-empts niche space that would otherwise be available (Vieites-Blanco and González-Prieto 2020). However, it might also be the case that these native shrubs are inhibiting *Acacia* invasion, rather than being outcompeted, and this highlights the difficulty in the determination of causality in such interactions (Cassini 2020). The coexistence of multiple nitrogen-fixing species in *Acacia*-invaded areas may be constrained, as increased *Acacia* dominance boosts nitrification rates, soil nitrogen availability, and canopy closure, thereby reducing microclimatic variability (i.e., a pattern observed in *A. dealbata*; Lorenzo et al. 2017). Interestingly, higher shrub cover in invaded areas was associated with improved litter and soil quality, as indicated by higher litter C/N ratios and increased SOC (Table 2). This is in line with a previous study showing that natural shrublands have been shown to act as barriers to *Acacia* invasion in the northern Iberian Peninsula (Rodríguez et al. 2017), and our results suggest that the density and identity of the shrub layer are key factors determining shrub vulnerability to *Acacia*'s competitive dominance.

Acacia invasion altered litter and soil quality (H_2)

The *Acacia* invasion had contrasting effects on litter and soil characteristics in the fragmented forest landscape. The reduction in litter C/N ratio and increase in SOC were likely driven by the chemical composition of *Acacia* litter because, as nitrogen-fixing species, *Acacia* can significantly affect soil properties (Liao et al.

2008; Lee et al. 2017), and persistent litter inputs may drive long-term alterations in soil conditions (Vivanco and Austin 2008; Souza-Alonso et al. 2015). Early in decomposition, *Acacia* litter contributes with labile organic carbon, while recalcitrant compounds resist rapid breakdown (Souza-Alonso et al. 2017, 2024). Species such as *A. dealbata* (Madureira and Ferreira 2022) and *A. melanoxylon* (González et al. 1995; Marchante et al. 2019; Pereira et al. 2021; Pereira and Ferreira 2022) produce litter with high lignin content, slowing down organic matter decomposition. However, these changes do not immediately translate into shifts in nutrient cycling or soil carbon pools, as organic matter turnover depends on thresholds of litter input and accumulation (Prescott and Zukswert 2016; Souza-Alonso et al. 2024). Furthermore, topographical gradients within the fragmented forest landscape played a significant role not only in shaping herb cover but also in influencing litter C/N ratio, likely through parallel mechanisms that modulate the niche requirements of the invader (Warren et al. 2011). Additionally, differences in the age and aboveground carbon stocks of *Acacia* stands may have further influenced the magnitude and timing of these effects (Matos et al. 2023). It is important to note, however, that *A. dealbata* litter generally does not accumulate as much as *A. melanoxylon* litter due to its more fragmented structure. *Acacia dealbata* has compound leaves, while *A. melanoxylon* produces sclerified phyllodes that decompose more slowly (Renner et al. 2021). Thus, their litter may influence C/N ratios and SOC accumulation in different ways. Distinguishing between these species in future studies at a landscape level could provide further insights into the mechanisms driving changes in litter and soil quality.

Absence of direct effects of *Acacia* invasion on springtails (H_3) but functional shifts driven by cascading changes in litter and soil (H_4)

Although *Acacia* invasion caused notable shifts in vegetation structure and litter and soil characteristics, its direct effects on springtail functional groups across the fragmented landscape were not significant. This broader pattern at the landscape level, however, contrasted with the more pronounced cascading effects observed in invaded sampling areas, where springtail functional structure was notably influenced by changes in litter and soil characteristics. Hemiedaphic springtails, in particular, showed a significant negative correlation with the litter C/N ratio. Their reliance on the formation of thick organic layers makes them sensitive to changes in abiotic conditions, and as intermediate dwellers in the soil-litter interface, they are highly dependent on litter quality, which shapes their microhabitats and provides essential food resources (Marian et al. 2018; Xie et al. 2024). A lower litter C/N ratio indicates higher proportional nitrogen content and greater litter palatability, making it richer in terms of nutrient availability (Gerlach et al. 2014; Nascimento et al. 2019). Therefore, the observed negative association between hemiedaphic springtail abundance and higher litter C/N ratios suggests that these springtails are favored by improved litter quality associated with lower C/N ratios. Meanwhile, euedaphic springtails, which inhabit deeper soil layers and are relatively independent of food or substrate quality (Krab et al. 2010), showed a positive response to increased SOC levels in the invaded sampling points. Predominantly parthenogenetic (i.e., reproducing without fertilization by a male), they are well-adapted to microhabitats with stable abiotic conditions like deeper soils, allowing for rapid population growth, particularly following disturbances (Lindberg and

Bengtsson 2005; Pollet et al. 2022). Moreover, the accumulation of SOC in these deeper layers was likely driven by slower decomposition rates and reduced microbial activity, conditions often associated with *Acacia* invasion (Lazzaro et al. 2014). Consequently, the interplay between their reproductive strategy and the altered soil environment likely underpinned their higher abundance in invaded areas with higher SOC levels.

Unlike hemiedaphic and euedaphic life forms, which are closely linked to variations in litter and soil conditions and were found in much higher numbers throughout the landscape, surface-dwelling epigeic springtails seemed to exhibit a reduced dependence on these factors. This reduced sensitivity may stem from their greater mobility, which allows them to exploit a wider range of microhabitats and makes them less constrained by microhabitat soil and litter characteristics (Martins da Silva et al. 2016). This result contrasts with the findings of Long et al. (2023), who showed that epigeic springtails were the only springtail functional group significantly affected by bamboo invasion. This discrepancy may be due to differences in the specific alterations originated by *Acacia versus* bamboo invasion, likely reflecting that the impacts of invasive alien plant species on belowground decomposers are context- and species-dependent (Luan et al. 2021).

It is important to note that we explored potential cascading effects of *Acacia* invasion on springtails through correlation analyses framed within a causal structure defined *a priori*. However, we acknowledge the limitations of this approach: while correlations are informative, they do not establish causality, and other processes not captured in our study, such as shifts in microbial activity or complex interactions within the soil food web (Potapov et al 2016; McCary and Wise 2019), may also influence springtail functional structure. These factors should be considered in future studies aiming to disentangle the full set of mechanisms underlying belowground responses to *Acacia* invasion.

Some methodological constraints may also partly explain the weak direct effects of *Acacia* invasion on springtail communities observed here. Although we sampled the upper 0–5 cm of soil (where springtails are typically concentrated) with a standardized 5 × 5 cm core, deeper layers were not assessed and might harbor additional species or invasion-driven shifts. Moreover, our functional trait-based approach captures the ecological consequences of community shifts without requiring the specialized expertise and resources needed for full species-level identification (Vandewalle et al. 2010; Moretti et al. 2017), but it cannot reveal taxonomic turnover in detail. Future work should consider deeper soil sampling and, where feasible, combine trait-based and taxonomic approaches to provide a more complete picture of invasion impacts on springtail diversity and function.

Implications towards a better management of *Acacia* invasion at a landscape level in the Mediterranean Basin

Our results showed that even low levels of *Acacia* invasion influenced vegetation structure and litter and soil quality within a fragmented forest landscape. These changes underline the profound and interconnected impacts of invasive species on both aboveground and belowground ecological processes, highlighting the cascading effects of *Acacia* invasions on ecosystem functioning.

Management efforts typically focus on the invasive species or the invaded community, but integrating the broader landscape context can improve intervention

strategies (Vilà and Ibáñez 2011). While *A. dealbata* currently causes stronger impacts due to its wider distribution, prioritizing areas with smaller infestations of either *A. dealbata* or *A. melanoxylon* is more effective for preventing further spread and impacts. Early intervention increases the likelihood of successful control, reduces costs, prevents negative effects and contributes to greater ecosystem stability. Regardless of the specific measures applied, follow-up management is essential, as both species have persistent, long-lived seed banks and can resprout after disturbances such as cutting or fire. Additionally, restoring native habitats is recommended. This is crucial not only to prevent the establishment of *Acacia* species in areas where they are absent, but also to detect them at early invasion stages and control them promptly, minimizing the risk of more severe ecological consequences (IPBES 2024).

Our results underscore the need for proactive measures to manage the *Acacia* invasion in the Mediterranean Basin, specifically in the case of *A. melanoxylon*, which remains more localized (Souza-Alonso et al. 2017), but also of *A. dealbata*, and other *Acacia* species in areas where they start to invade. In particular, our studied fragmented forests in Central Portugal, where *A. dealbata* is already widespread but also found in more localized areas, and *A. melanoxylon* is still confined to smaller patches, present an opportunity for early intervention to prevent further spread and impacts of both species.

Acknowledgements

We would like to thank all the volunteers who helped with field and lab work. We also thank Aflopinhal – Associação Florestal do Pinhal for the logistic support during field work. We thank the editor Elizabeth Wandrag, one anonymous reviewer, and Florencia Yannelli for their valuable comments that helped improve the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This work was funded by the project "F4F – Forest for Future – Pilot project for the constitution of a regional network for the valorisation of the forest sector in the Central Region. PP6 – MyFOREst (Ref. CENTRO-08-5864-FSE-000031)", co-financed by the Regional Operational Programme Centro 2020, Portugal 2020, and the European Union, through the European Social Fund (ESF). R. Juan-Ovejero holds a postdoctoral contract (Ref. ED481B-2022-006) funded by the Consellería de Cultura, Educación, Formación Profesional e Universidades from the Xunta de Galicia. J. Alves was funded by FCT – Fundação para a Ciência e a Tecnologia, I.P. under Scientific Employment Stimulus Individual support (2022.05848.CEEIND; DOI: https://doi.org/10.54499/2022.05848.

CEECIND/CP1714/CT0008). This study was partially funded by the FCT through the strategic projects of the Centre for Functional Ecology – Science for People and the Planet (CFE) (UIDB/04004/2025), and Associate Laboratory TERRA (LA/P/0092/2020; DOI: https://doi.org/10.54499/LA/P/0092/2020).

Author contributions

Conceptualization: RJO; PMS. Formal analysis: RJO; PMS. Data curation: RJO; FR; FG; FC; MCD. Visualization: RJO; EM; PMS. Funding acquisition: JA; JPS; HF. Investigation: RJO; FR; FG; FC; MCD, AAS. Methodology: AAS; JPS, JA. Supervision: JA. Project Administration: JA. Writing – original draft: RJO. Writing – review and editing: EM; PMS; FR; FG; MCD; FC; HF; JA.

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Data availability

All of the data that support the findings of this study are available in the main text within tables and figures and in the Supplementary material.

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Supplementary material 1

Supplementary information

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Data type: docx

Explanation note: **table S1.** Cover (%) of each plant taxon at each of the 1 km^2 sampling points in the regular 25 km^2-grid at the Lousã mountains. **table S2.** Springtail functional type codes showing different morphotypes (from m02000 to m44444) and the total number of specimens (n) identified across the regular 25 km^2-grid at the Lousã mountains. **table S3.** Spearman correlation coefficients (ϱ) showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) cover and latitude, longitude, elevation, slope and aspect. **table S4.** Model selection for each response variable and for each tested hypothesis (H_1, H_2, and H_3). **table S5.** Similarity percentage (SIMPER) analysis of plant community assemblages in *Acacia*-invaded (n = 9) versus non-invaded (n = 16) sampling points. **fig. S1.** Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis similarity index of the plant community assemblages in *Acacia*-invaded (n = 9) and non-invaded (n = 16) sampling points. **fig. S2.** Scatterplots showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance with herb cover. **fig. S3.** Scatterplots showing the relationships between the proportion of *Acacia* (*A. dealbata* + *A. melanoxylon*) relative to total tree abundance with litter C/N ratio.

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